SEED AND SEEDLING ECOPHYSIOLOGY OF NEOTROPICAL MELASTOMATACEAE: IMPLICATIONS FOR CONSERVATION AND RESTORATION OF SAVANNAS AND RAINFORESTS[1]

Fernando A. O. Silveira,[2,3] *G. Wilson Fernandes,*[3] *and José P. Lemos-Filho*[2]

Abstract

We review the patterns of fruit maturation, dispersal, germination, seed bank formation, and seedling establishment of the Melastomataceae in two Neotropical biodiversity hotspots, the Brazilian cerrado and the Atlantic rainforest. Studies on seed biology of the Melastomataceae are relevant because this family is ubiquitous, species-rich, and dominant in these two hotspots, and its increased relative importance is anticipated under the current scenario of habitat loss and forest fragmentation. The life-history traits of this pioneer-dominated family are quite variable in terms of fruiting phenology and seedling establishment, but less so for dispersal ecology and seed germination. Our knowledge of this seed biology is used to infer on the predicted impacts of global change and forest fragmentation for tropical forest and cerrado melastomes. Species in the Melastomataceae may be key in restoration ecology, and we discuss how seed- and seedling-based restoration techniques can assist ecosystem recovery.

Resumen

Revisamos los patrones de maturación de frutos, dispersión, germinación, banco de semillas y establecimiento de plantas de Melastomataceae en dos hotspots debiodiversdad, el cerrado y la Mata Atlántica. Estudios de semillas de Melastomataceae son importantes porque la familia presenta alta diversidad y es dominante en un gran rango de hábitats. Además, resulta que la familia tiene prevista su importancia aumentada en escenarios de fragmentación de bosques. Las características de história de vida de esta familia de plantas pioneras es muy variable con respecto a la fenología reproductiva y establecimiento de plántulas, pero no tanto con respecto a la ecología de dispersión de semillas y germinación. La biología de semillas embasa la discusión sobre los impactos de los cambios globales y fragmentación de bosques en Melastomataceae de sabanas y bosques tropicales. Especies de Melastomataceae pueden ser claves para la ecología de la restauración y discutimos como las técnicas de restauración basadas en semillas y plántulas pueden ayudar en la restauración.

Key words: Forest fragmentation, global change, Melastomataceae, Neotropics, seed bank, seed dispersal, seedling establishment, seed germination.

Patterns of seed germination have important ecological and evolutionary implications. Germination patterns affect population dynamics, individual fitness (Verdú & Traveset, 2005; Donohue et al., 2010), and species geographic distribution and abundance (Donohue et al., 2010), ultimately leading to changes at the community level. Patterns and processes relative to seed germination have also been used to explain intraspecific competition (Verdú & Traveset, 2005), coexistence of sympatric species (Grubb, 1977), and ecological breadth and geographic range (Donohue et al., 2010), hence highlighting the role of germination in structuring plant communities. Moreover, knowledge of seed biology is integral to our understanding of processes such as plant establishment and natural succession and

[1] We thank D. Negreiros, L. M. Araújo, and N. C. Robles for help during experiments and J. R. Stehmann for providing important bibliography on the Atlantic forest. We also thank M. A. Pizo, C. C. Baskin, A. C. Franco, and three anonymous reviewers for important comments on earlier versions of the manuscript. V. C. Hollowell made important editorial changes to the text. We are indebted to R. Romero, A. B. Martins, and R. Goldenberg for plant identification and to L. C. Martins for editing the figures. The authors acknowledge scholarships and financial support from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), and Fundação de Amparo à Pesquisa do estado de Minas Gerais (FAPEMIG).

[2] Departamento de Botânica/ICB/Universidade Federal de Minas Gerais, CP 486, 30161-970 Belo Horizonte, Minas Gerais, Brazil. faosilveira@gmail.com

[3] Ecologia Evolutiva & Biodiversidade/DBG, ICB/Universidade Federal de Minas Gerais, CP 486, 30161-970 Belo Horizonte, Minas Gerais, Brazil.

doi: 10.3417/2011054

contributes to the development of a theoretical framework for restoration ecology (Vásquez-Yanes & Orozco-Segovia, 1993). Herein, we review the available evidence on seed development, dispersal, predation, germination, and seedling ecophysiology of cerrado and Atlantic forest Melastomataceae. Finally, we briefly discuss how knowledge of seed and seedling ecology of melastomes may be applied to conservation and restoration.

The Brazilian Cerrado and Atlantic Forest

The effects of human activities have considerably diminished the Brazilian cerrado and Atlantic forest in their areas of coverage. The cerrado covers nearly two million km^2, representing 22% of the land surface of Brazil and occupies an altitudinal range from near sea level to 1800 m.s.m. (Oliveira-Filho & Ratter, 2002). The cerrado developed on highly weathered low pH soils, which were aluminum-rich and poor in nutrients (Ratter et al., 1997). The climate is seasonal, marked by dry winters from April to September and rainy summers from October to March (Oliveira-Filho & Ratter, 2002). Typical cerrado vegetation landscape consists of a complex mosaic of savanna physiognomies on well-drained interfluves with riparian forests along watercourses. Physiognomies range from dense grasslands with shrubs and small trees sparsely interspersed (Fig. 1A) to almost closed woodlands (Ratter et al., 1997). Both woody and herbaceous flora developed traits typical of pyrophytic savanna vegetation. The trees are of a low contorted form, with thick, corky, fire-resistant bark and sclerophyllous leaves and underground perennating organs (Simon et al., 2009). Soil erosion, land degradation, uncontrolled fires, and invasive species, along with increases in cleared areas for agriculture, pasture, and charcoal production threaten cerrado biodiversity. Deforestation rates are higher in the cerrado than in the Amazon forest, whereas conservation efforts have been modest: only 2.2% of the cerrado area is currently under legal protection (Klink & Machado, 2005).

The Atlantic forest originally covered ca. one million km^2, extending throughout the Brazilian coast. The biome is composed of two major vegetations: the Atlantic rainforest, which covers mostly the low to medium elevations (< 1000 m.s.m.) along the South American coastline; and the Atlantic semi-deciduous forest that extends toward the west, across the Brazilian plateau in the central and southeastern interior of the continent (Morellato & Haddad, 2000; Oliveira-Filho & Fontes, 2000). The south–north orientation of the coastline and mountain ranges gives rise to orographic rains, resulting in an ever-wet rainforest climate, with annual precipitation exceeding 2000 mm. The relative humidity is higher than 85% year round and the mean annual temperature is nearly 22°C (Morellato et al., 2000). The Atlantic forest has been subjected to intense human pressures, and only a small portion of its original area of coverage remains (ca. 11.4%–16%) as small and isolated fragments (Ribeiro et al., 2009: 1145).

Melastomataceae in the Cerrado and Atlantic Forest

The Melastomataceae comprise shrubs, climbers, herbs, epiphytes, or trees that occur from montane to lowland forests and in savannas and disturbed vegetation (Clausing & Renner, 2001). This pantropical family comprises 4570 species in 150 to 166 genera arranged into nine tribes (Renner, 2004) and attains its highest taxonomic diversity in the Neotropics with ca. 3000 species (Renner et al., 2001). The Melastomataceae is the fourth most speciose family in the cerrado (Mendonça et al., 2008). Melastome diversity is high in both herbaceous and woody communities (Ratter et al., 1997), significant in terms of species number, area of occurrence, aerial cover (Jacobi et al., 2007), and endemism (Romero & Martins, 2002). Representative taxa include the Miconieae, Microlicieae, and Melastomeae (Mendonça et al., 2008). Miconieae, the most species-rich tribe, is a monophyletic tribe characterized by inferior or partly inferior ovaries that develop into baccate fruits (Goldenberg et al., 2008). Nearly 90% of the estimated 275 to 300 species of Microlicieae originated in and are endemic to the cerrado (Fritsch et al., 2004; Simon et al., 2009). Melastomeae is characterized by having stamens with a pedoconnective, appendages ventral and paired when present, and capsular fruits that contain cochleate seeds with curved embryos (Michelangeli et al., 2013). This tribe includes at least 870 species in 47 genera. Most threatened species belong to endemic Microlicieae (Mendonça & Lins, 2000).

The Melastomataceae is amongst the most important families in the woody flora of the Atlantic forest. *Miconia* Ruiz & Pav. and *Tibouchina* Aubl. are the dominant genera in both Atlantic rainforest and semi-deciduous forests (Oliveira-Filho & Fontes, 2000). The family is diverse both in lowland and montane forests in northeastern Atlantic forest (Cavalcanti & Tabarelli, 2004). Gap specialist shrubs and shade-tolerant trees in Melastomeae and Miconieae account for the highest diversity, but species in Bertolonieae and Henrietteae are also important. The Microlicieae is species-poor in the Atlantic forest (Fritsch et al.,

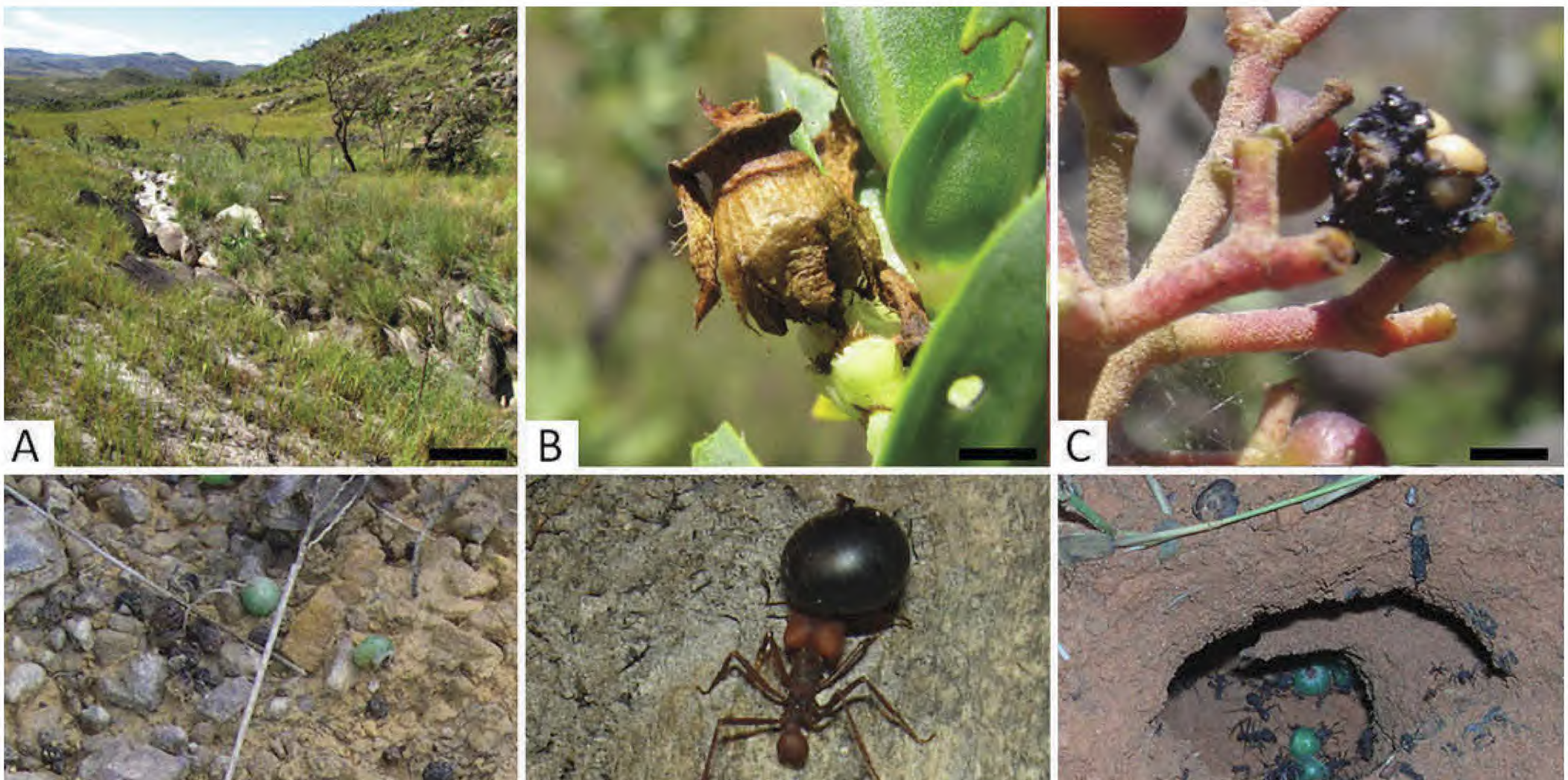


Figure 1. Bird and ant frugivory in *Miconia* Ruiz & Pav. —A. General view of a campo rupestre (altitudinal rocky grassland). —B. Dry capsule of *Lavoisiera confertiflora* Naudin showing the base-to-apex dehiscense. —C. Mashed fruit of *M. irwinii* Wurdack in campo rupestre. —D. Fresh and rotten fruits of *M. albicans* (Sw.) Steud. fallen beneath parent plant. —E. *Atta sexdens* L. soldier carrying *M. irwinii* berry. —F. Fallen fruits of *M. albicans* near *A. sexdens* nest. —G. Attini ant chewing on a fruit stalk. —H. Infructescence of *M. albicans* galled by *Ditylenchus gallaeformans*, leaving no unattacked fruits —I. Early seedling establishment in the campo sujo. Photo of E taken by M. H. C. Lima; all other photos taken by F. A. O. Silveira. Scale bar for A = 1 m, B = 0.4 cm, C–E, I = 1 cm, F = 2 cm, G = 0.5 cm, and H = 2 cm.

2004). New World Melastomeae occupies a variety of forest vegetation types including lowland and cloud forests and some species occupy seasonally flooded habitats (Michelangeli et al., 2013).

FROM FLOWER TO FRUIT

The pollination biology and breeding system of the Melastomataceae have been reviewed by Renner (1989). The Miconieae shows a disproportional occurrence of apomictic species with respect to the other tribes (Goldenberg & Shepherd, 1998; Mendes-Rodrigues & Oliveira, 2012), and seeds obtained from apomictic species are able to germinate normally. Polyembryony is often associated with apomictic widespread species in South America (Mendes-Rodrigues & Oliveira, 2012).

Seeds of the Melastomataceae are small to minute in size and lack endosperm. Mature seeds are exarillate and exalbuminous (Baumgratz, 1985). Most seeds are typically between 0.4 and 2 mm in length, and seed mass is generally less than 0.01 g (an exception is *Mouriri* Aubl., for which fruits are 0.5–10 cm long; Renner, 1989). Fully developed embryos consist of a conspicuous embryonic axis and two fleshy cotyledons (Baumgratz, 1985; Silveira et al., 2012b). The radicles are short and hardly distinguishable from the hypocotyl. Phenolic compounds generally occur in the seed coats, in cell walls, or in the vacuoles (Silveira et al., 2012b). The embryos are

often bent, folded, investing, linear, and/or spatulate (Baskin & Baskin, 2007, Silveira et al., 2012b), and completely fill the seed, resulting in a high embryo to seed ratio (Forbis et al., 2002).

Fruit and seed maturation studies provide the initial basis for understanding germination ecology. Melastomes produce an unusual diversity of fruit types including woody berries, fleshy capsules, and capsules containing fleshy placentas, but for simplicity we refer only to berries and capsules. Melastome capsules and berries have evolved independently several times within the family (Clausing et al., 2000). Fruit character plasticity in the Melastomataceae may relate to shifts in seed dispersal mechanisms, which in turn relate to the type of habitat and dispersal agent. Thus, changes from fleshy berries to dry capsules may correlate with colonization of more open habitats where wind dispersal is more effective than animal dispersal (Clausing et al., 2000). Alternatively, capsular-fruited species may undergo selection for increased exocarp and placenta fleshiness in more closed-forest habitats where vertebrate dispersal predominates (Clausing et al., 2000). Animal-dispersed melastomes are more diverse in forests, whereas capsular-fruited groups are richer in savannas (Stiles & Rosselli, 1993).

The extent of berry maturation (the time between pollination and ripening) greatly varies among the Melastomataceae, with most species showing an irregular pattern of fruit maturation within the canopy and inflorescence (Pereira & Mantovani, 2001). Such a period of fruit and seed maturation may extend from 100 to 220 days after anthesis (DAA) for fleshy-fruited species (Carreira, 2004). In *Tibouchina mutabilis* (Vell.) Cogn., 10% of dry seeds were viable at 14 DAA, and a high percentage of viable seeds was observed 21 DAA (Simão et al., 2007). Mature seeds of *T. granulosa* (Desr.) Cogn. were harvested only between 84 and 105 DAA (Lopes et al., 2005). As for berries, their tissues remain hydrated (70%–80%, water content) and accumulate sugars (Lima et al., 2013). Germination inhibitors occur in unripe and ripe berries of several *Miconia* species (Amaral & Paulilo, 1992; Carreira, 2004; Silveira et al., in prep), which suggests that seed cleaning by frugivores is required prior to germination (Silveira et al, 2012a; Lima et al., 2013). Seed water content at maturity was noted as 27% for *Miconia albicans* (Sw.) Steud. (Carreira, 2004) and 23% for *M. cinnamomifolia* (DC.) Naudin (Lopes & Soares, 2006) and *T. granulosa* (Lopes et al., 2005). Recalcitrance has been reported only for *Melastoma malabathricum* L. from tropical swamp forests (Farnsworth, 2000).

Malformed and well-developed but embryoless seeds (WELS) are commonplace in the family (Baumgratz, 1985). Quantitative data are lacking perhaps because of the difficulty of evaluating viability among the small-seeded species. The percentage of WELS ranges from 13% to 86.5% and varies across lineages including *Tibouchina* (Zaia & Takaki, 1998; Simão & Takaki, 2008; Silveira et al., 2012b), *Trembleya* DC. (Rodrigues & Silveira, 2013), *Miconia* (Mendes-Rodrigues et al., 2010; Silveira et al. 2012b; Silveira et al., in prep.), *Marcetia* DC. (Vasconcelos et al., 2007), *Chaetostoma* DC., and *Comolia* DC. (Silveira et al., 2012b).

From the Mother Plant to Soil

Seed dispersal is strongly influenced by life-history traits and fruit morphology. Fruits are structurally diverse in the Melastomataceae, and dispersal mode varies as a function of fruit morphology (Clausing et al., 2000). Nearly 40% of Neotropical melastomes have capsular fruits, whereas 60% have endozoochorous berries (Renner, 1989). Species in the Miconieae are animal-dispersed, whereas Melastomeae and Microlicieae are abiotically dispersed (Silveira, 2011). Apart from differences in fruit morphology, melastomes are also diverse in their reproductive phenology.

FRUITING PHENOLOGY

In the Amazon forest, reproductive phenology of melastomes tends to occur continuously throughout the year (Renner, 1986–1987, but see Paarmann et al., 2002). However, fruiting phenology in Atlantic forest trees is variable (Morellato et al., 2000), as exemplified by Miconieae. In the lowland Atlantic forest, *Leandra* sp. indet., aff. *sublanata* Cogn. (Gridi-Papp et al., 2004), *Miconia dodecandra* Cogn., and *Tibouchina pulchra* (Cham.) Cogn. fruit year round, whereas *M. prasina* (Sw.) DC., *M. rigidiuscula* Cogn. (Talora & Morellato, 2000), *M. cinnamomifolia* (Mantovani et al., 2003), *M. cinerascens* Miq. (Gridi-Papp et al., 2004), and *M. hypoleuca* (Benth.) Triana (Galetti & Stotz, 1996) fruit only during the dry season (June to August). *Miconia cabussu* Hoehne (Mantovani et al., 2003) and *M. urophylla* DC. (Manhães et al., 2003), in turn, fruit during the rainy season of November to March. The predominant aseasonal fruiting phenology of melastomes in the Atlantic rainforest suggests that climatic factors do not limit fruit production in forest trees. Rather, competition for frugivores may be a stronger selective pressure, and, thus, in the Atlantic forest, fleshy fruits are available year round for frugivores

(Morellato et al., 2000). Staggered fruiting seasons may have competitively evolved in *Miconia* species that share similar animal-dispersal agents (Snow, 1965). Melastome berries are regarded as a key resource for Neotropical frugivorous birds, providing them with otherwise limited water and sugar-based resources (Stiles & Rosselli, 1993; Galetti & Stotz, 1996). Fruiting phenologies of forest *Miconia* from other sites in South America are also segregated over time (Poulin et al., 1999; Kessler-Rios & Kattan, 2012), supporting the hypothesis that segregated fruiting may have evolved through interspecific competition (Snow, 1965).

Within the cerrado, however, seedling establishment is assumed to be constrained during the dry winters, with selective pressure for temporal shifts of reproductive phenophases during the onset of the rainy season. Thus, the synchronization of seed dispersal near or during the onset of the rainy season (that period of high soil moisture) is believed to increase seedling survival and reduce drought-induced mortality (Oliveira, 2008). Unfortunately, there are too few phenological studies on cerrado melastomes (Lopes et al., 2005; Montoro & Santos, 2007; Simão et al., 2007; Garcia et al., 2009) to determine whether fruiting patterns found for forest melastomes are similar to those from the cerrado. There is some preliminary evidence suggesting staggered fruiting in cerrado Miconieae (Maruyama et al., 2007; Silveira et al., unpublished data).

Dispersal Ecology

Data on abiotic dispersal of melastome capsules are scarce. Even though most capsular-fruited melastomes are thought to be wind-dispersed (Silveira, 2011; Fig. 1B), rainfall is needed to release the seeds from the capsules of *Bertolonia mosenii* Cogn. and probably other Bertolonieae (Renner, 1989; Pizo & Morellato, 2002). The distance of the anemochoric dispersal in such melastomes is currently unclear. Berries from riparian *Tococa* Aubl. species that fall into the water and float further into moist forest habitats represent another example of abiotic dispersal. Pubescent seeds may be adaptations to water and/or fish dispersal (Michelangeli, 2005).

Most Miconieae produce small black, red, or blue berries (Renner, 1989). Berries of the Miconieae usually have fleshy placentas and fused tissues or carpels and other accessory structures (Cortez & Carmello-Guerreiro, 2008) in which numerous small seeds are embedded (Silveira et al., 2012b; Lima et al., 2013). Such melastome berries fall into the category of generalist fruits, typically characterized by small size (5–35 mm diam., Renner, 1989), high fecundity, small seed size, and low protein content (McKey, 1975). Such small berries with high water and sugar content are consumed by small frugivorous and omnivorous birds in several families (McKey, 1975; Renner, 1989; Michelangeli, 2005; Schupp et al., 2010; Kessler-Rios & Kattan, 2012).

In Costa Rican, Amazonian, and Atlantic forests, Tyrannidae (fly-catchers), Pipridae (manakins), Turdidae (thrushes), and Thraupidae (tanagers) are major avian frugivores (Loiselle & Blake, 1999). However, the Pipridae are species poor in the cerrado (Macedo, 2002). Large birds in Cracidae (chachalacas, guans, and curassows), Columbidae (doves and pigeons), and Ramphastidae (toucans) play a minor role in fruit removal in South America (Renner, 1989). Fruits of *Mouriri elliptica* Mart., found in the cerrado, are argued to be anachronic (fruits with apparent ex-adaptations to the extinct South American megafaunal community; Guimarães et al., 2008).

The understory melastomes in Costa Rican rainforests have a relatively small set of seed dispersers in contrast to those for canopy trees. Effective dispersers are essentially composed of two or three species, and plant–bird interactions may be more specific in forest understory than in species-rich canopies (Loiselle & Blake, 1999). Brazilian melastome shrubs are visited by a larger assemblage of generalist frugivores (Galleti & Stotz, 1996; Pereira & Mantovani, 2001; Marcondes-Machado, 2002; Manhães et al., 2003; Michelangeli, 2005).

Effects of frugivores on seeds and seedlings

Fruit consumption by frugivores does not necessarily mean that seeds are dispersed because ingested seeds can be damaged by gut passage. The effect of such dispersal can be measured in quantitative and qualitative components (sensu Schupp et al., 2010). Birds are not alike in their ecological roles as seed dispersers for shrubs in the Melastomataceae, differing in both dispersal quantity and quality (Loiselle & Blake, 1999). Removal rates are typically low by manakins and tanagers (Blendinger et al., 2008). The two groups differ in feeding ecology, as the former gulp, eating the fruit whole (high dispersal quantity), and the latter mash and drop seeds near the parent plant (low dispersal quantity; see Fig. 1C) where seed survival is reduced by density-dependent mortality (Stiles & Rosselli, 1993).

Seed cleaning by frugivores improves dispersal quality by removing inhibition factors. The inhibition effect arises from low osmotic potential caused by the high sugar content of ripe fruits, light-blocking pigmentation that prevents enough light reaching

the seeds, and secondary metabolites that directly inhibit seed germination (Samuels & Levey, 2005). Germination inhibitors in fruits of several *Miconia* species (Amaral & Paulilo, 1992; Carreira, 2004) suggest the widespread occurrence of these compounds in the family, though their chemical nature still awaits determination. Seeds within intact melastome fruits (Fig. 1D) rarely germinate (Silveira et al., 2012a), making seed cleaning beneficial for recruitment. Finally, pulp removal may help decrease the probability of pathogen-induced seed death; intact fruits show extensive signs of fungi infestation (Silveira et al., 2012a). The pulp removal and consequent removal of inhibitory compounds are provided by gulpers and to a lesser extent by mashers.

Seed passage through frugivore guts causes differing effects on germination. Seed retention time inside the disperser and the morphology and physiology of its digestive tract may all affect the survival probability of ingested seeds (Traveset el al., 2007). Intact seeds of *Tococa* and *Miconia* have been retrieved after gut passage of fishes (Michelangeli, 2005) and coatis (*Nasua nasua* L., Alves-Costa & Eterovick, 2007), but the lack of germination trials prevents attempts to link dispersal with recruitment. Germinability of seeds from rodent scats was not affected (Lessa & Costa, 2009), but was improved after marsupial gut passage (Lessa & Costa, 2010).

The effects of gut passage of several Costa Rican melastomes after ingestion by the red-capped manakin *Pipra mentalis* Sclater ranged from positive to negative (Ellison et al., 1993). Overall for forest (Manhães et al., 2003; Alves et al., 2008; Gomes et al., 2008) and cerrado species (Silveira et al., 2012a), seed passage through bird gut has minor effects on germination. The seeds of *Clidemia hirta* (L.) D. Don were thought to be dormant, requiring bird ingestion for dormancy break (Pereira-Diniz, 2003). For this species, there was indeed a positive effect of gut passage on germination (Linnebjerg et al., 2009), but data did not support the hypothesis of seed dormancy.

Other primary and secondary dispersers

Birds are the main dispersers of melastomes, but mammals are also important primary seed dispersers. Berries are eaten by bats, monkeys (Renner, 1989; Galleti & Stotz, 1996; de Figueiredo & Longatti, 1997; Garcia et al., 2000; Lapenta & Procópio-de-Oliveira, 2008), rodents, marsupials (Magnusson & Sanaiotti, 1987; Lessa & Costa, 2009, 2010), and coatis (Alves-Costa & Eterovick, 2007). A large portion of the fruit produced by Miconieae is not removed by primary dispersers. Fruits fallen to the ground are eaten by turtles, lizards, tapirs (Renner, 1989), and armadillos (Baumgratz et al., 2006). Nevertheless, ants are the most important seed consumers of fallen fruits (Fig. 1E, 1F). Ants actively forage on soil in search for small-sized diaspores or even climb in the plants to cut fruit stalks (Fig. 1G). Fungus-growing ants (Attini) transport *Miconia* fruits in the cerrado (Christianini & Oliveira, 2009; Lima et al., 2013) and also remove seeds from bird feces (Leal & Oliveira, 1998; Christianini & Oliveira, 2009). Interactions between ants and fallen melastome fruits may be especially common in lowland rainforests in which ant abundance is coupled with year-round availability of fleshy fruits (Dalling & Wirth, 1998; Pizo & Oliveira, 2000).

Potential benefits of ants to non-myrmecochorous melastomes include seed cleaning, increased germination success, reduced damage to seeds and seedlings, and reduced sibling competition (Rico-Gray & Oliveira, 2007). Because seeds within fallen fruits are less likely to germinate (Fig. 1D), pulp removal and subsequent reduction in fungal infestation (Samuels & Levey, 2005; Rico-Gray & Oliveira, 2007) may be an important benefit emerging from ant–melastome interactions. Fruit displacement may increase the chances of seeds reaching safe sites, and seed deposition in refuse piles may provide seedlings with a suitable substrate for establishment (Lima et al., 2013). Because seed delivery patterns by ants are likely to differ from those of birds, ants may influence species population dynamics and spatial distribution (Christianini & Oliveira, 2009).

From Seed to Seedling: Effects of Light and Temperature

Light and temperature are among the most significant abiotic factors controlling seed germination (Heschel et al., 2007). Here, we focus on how melastome seeds respond to these abiotic stimuli. Despite the relatively few species reviewed (29 species in eight genera, Table 1), a general pattern for seed germination in the Melastomataceae emerged. Under controlled conditions, seeds of the 25 species investigated were uniformly and positively photoblastic. Germination of melastome seeds under dark conditions is negligible, irrespective of phylogenetic position, geographic distribution, growth form, or temperature (Silveira, 2011).

Extreme temperatures seem to be deleterious for melastome germination, with only 33% of cerrado species and 40% of Atlantic forest species germinating at temperatures above 30°C (see Table 1). Optimum temperature (which allows faster and maximum germination) is reported for only 62% of

Table 1. The effect of light and temperature on germination of Melastomataceae seeds from Brazilian cerrado and Atlantic forest. *Tibouchina heteromalla* is the only taxon considered from both biomes and *Miconia cinnamomifolia* and *T. granulosa* appear twice because they represent accessions for two different studies.

Biome	Tribe	Species	Maximum G (%)[a]	Temperature range	Optimum temperature	Light response	Dormancy type	Reference
AF	Melastomeae	*Tibouchina benthamiana* (Gardner) Cogn.	~70	20–30	30	L > D	ND	Andrade, 1995
AF	Melastomeae	*T. granulosa* (Desr.) Cogn.	24.9	NA	NA	L > D	ND	Zaia & Takaki, 1998
AF	Melastomeae	*T. granulosa* (Desr.) Cogn.	17	NA	NA	L > D	ND	Lopes et al., 2005
AF	Melastomeae	*T. heteromalla* (D. Don) Cogn. [= *T. grandifolia* Cogn.]	~60	15–35	25–30	L > D	ND	Andrade, 1995
AF	Melastomeae	*T. moricandiana* Baill.	~70	20–30	25	L > D	ND	Andrade, 1995
AF	Melastomeae	*T. mutabilis* (Vell.) Cogn.	~80	15–35	25–30	L > D	ND	Simão & Takaki, 2008
AF	Melastomeae	*T. pulchra* Cogn.	30.9	NA	NA	L > D	ND	Zaia & Takaki, 1998
AF	Melastomeae	*T. sellowiana* Cogn.	NA	NA	30	L > D	ND	Barbosa et al., 1988
AF	Miconieae	*Leandra breviflora* Cogn.	78	NA	NA	L > D	ND	Andrade, 1995
AF	Miconieae	*Miconia chamissois* Naudin	90	NA	NA	L > D	ND	Valio & Scarpa, 2001
AF	Miconieae	*Miconia cinnamomifolia* (DC.) Naudin	58.7	NA	25	L > D	ND	Pereira & Mantovani, 2001
AF	Miconieae	*Miconia cinnamomifolia* (DC.) Naudin	~60	20–30	25–30	L > D	ND	Amaral & Paulilo, 1992
AF	Miconieae	*Miconia urophylla* DC.	~60	NA	NA	L > D	ND	Manhães et al., 2003
CE	Melastomeae	*Marcetia candolleana* A. K. A. Santos & A. B. Martins	2	NA	NA	NC	NC	Vasconcelos et al., 2007
CE	Melastomeae	*Marcetia harleyi* Wurdack	2	NA	NA	NC	NC	Vasconcelos et al., 2007
CE	Melastomeae	*Marcetia macrophylla* Wurdack	1	NA	NA	NC	NC	Vasconcelos et al., 2007
CE	Melastomeae	*Marcetia shepherdii* A. B. Martins	2	NA	NA	NC	NC	Vasconcelos et al., 2007
CE	Melastomeae	*Marcetia taxifolia* (A. St.-Hil.) DC.	51	15–30	15–25	L > D	ND	Silveira et al., 2004
CE	Melastomeae	*T. gracilis* (Bonpl.) Cogn.	~75	15–35	25–30	L > D	ND	Carreira & Zaidan, 2007
CE	Melastomeae	*T. heteromalla* (D. Don) Cogn. [= *T. multiflora* Cogn.]	73	15–30	25–30	L > D	ND	Garcia et al., 2006
CE	Melastomeae	*T. papyrus* (Pohl) Toledo	70	NA	NA	NA	ND	Montoro & Santos, 2007
CE	Miconieae	*Clidemia hirta* (L.) D. Don	96	NA	NA	L > D	NC	Pereira-Diniz, 2003
CE	Miconieae	*Miconia albicans* (Sw.) Steud.	~80	15–35	20–30	L > D	ND	Carreira & Zaidan, 2007
CE	Miconieae	*Miconia ferruginata* DC.	59.5	NA	NA	L > D	NC	Mendes-Rodrigues et al., 2010
CE	Miconieae	*Miconia paucidens* DC. [= *Miconia langsdorffii* Cogn.]	~65	15–30	25	L > D	ND	Carreira & Zaidan, 2007
CE	Miconieae	*Miconia rubiginosa* (Bonpl.) DC.	~30	20–35	25	L > D	NC	Carreira & Zaidan, 2007
CE	Miconieae	*Miconia stenostachya* DC.	~65	15–35	20–30	L > D	ND	Carreira & Zaidan, 2007
CE	Miconieae	*Miconia theaezans* (Bonpl.) Cogn.	98	15–32.5	15–32.5	L > D	ND	Godoi & Takaki, 2007
CE	Microlicieae	*Lavoisiera cordata* Cogn.	~85	15–30	20–30	L > D	ND	Ranieri et al., 2003
CE	Microlicieae	*Lavoisiera imbricata* Cogn.	~35	15–30	25	L > D	ND	Ranieri et al., 2003
CE	Microlicieae	*Trembleya laniflora* (D. Don) Cogn.	16.5	15–30	20	L > D	ND	Rodrigues & Silveira, 2013

Abbreviations: L, Light conditions; D, dark; ND, seed nondormancy; D, dormancy; NC, nonconclusive; NA, data are not available.
[a] Percentages not corrected for viability.

the 29 species. Optimum temperature ranged from 20°C to 30°C, with the variable range of 15°C–32.5°C exhibited by *Miconia theaezans* (Bonpl.) Cogn.. Widespread species (*M. albicans*, *M. stenostachya* DC., and *M. theaezans* in cerrado, *Tibouchina mutabilis* in Atlantic forest, and *T. heteromalla* (D. Don) Cogn. in both biomes) were eurythermic, germinating over broad temperature ranges. However, contrary to predictions of the niche breadth hypothesis (Grubb, 1977), endemic species such as *Trembleya laniflora* (D. Don) Cogn., *Lavoiseria cordata* Cogn. ex Glaz., and *L. imbricata* DC. did not show narrow temperature ranges.

The positive photoblastic response of melastome seeds is typical of small-seeded, pioneer species in the Neotropics with seeds that preferentially germinate under forest gaps (Pearson et al., 2002, 2003a; Daws et al., 2008). The response of seed germination to red and far-red light is mediated by phytochromes. Melastome seeds have phytochrome B (*phyB*), which particularly influences germination under shaded or low-fluence conditions (Godoi et al., 2009). This photoregulator responds to differences in red and far-red wavelengths, as altered by canopy gaps (Casal & Sanchez, 1998); *phyB* affects germination despite a broad range of temperatures (Heschel et al., 2007). In the Atlantic forest, the red to far-red light (R:FR) ratios can drop significantly from 1.21 in open areas to 0.28 under closed canopy (Zaia & Takaki, 1999). Low R:FR light ratios under closed canopy may deter germination, and photoblastic seeds would accumulate in soil seed banks until canopy openings. The R:FR threshold for melastome seeds can be as low as 0.12 for *Miconia argentea* (Sw.) DC. (Pearson et al., 2003b). The amount of daily insolation also influences Melastomataceae germination. Melastome seeds require at least 60 minutes of daily irradiation to germinate (Carreira & Zaidan, 2007).

Effects of Fluctuating Temperatures

Temperature fluctuations may alter the responses of seeds to light such that photoblastic seeds can germinate in darkness when submitted to alternating temperatures (Pearson et al., 2002). Increased germinability of small-seeded species as a response to fluctuating temperature can be predicted because seeds buried at shallow soil depths would experience higher daily thermal fluctuations compared to more deeply buried seeds. Forest gaps would also increase daily temperature fluctuations in upper soil layers, relative to deeper soil, and seeds may cue for this variation (Pearson et al., 2002, 2003b). However, alternating temperatures do not promote germination of Neotropical melastomes nor could daily fluctuations in temperature be a surrogate for the light requirement (Carreira & Zaidan, 2007; Godoi & Takaki, 2007; Simão & Takaki, 2008). Among those species investigated (see Table 1), *Miconia chamissois* Naudin is the only taxon that apparently benefitted from alternating temperatures under optimal light conditions. When alternating daily temperatures include extremes, such as 35°C, germinability of melastomes is not observed (Godoi & Takaki, 2007). Daily variation in temperatures has been shown to favor germination of tropical large-seeded pioneers (Válio & Scarpa, 2001; Pearson et al., 2002), but for Neotropical Melastomataceae, alternating temperatures have a minor role in seedling emergence.

SEED DORMANCY

A completely nondormant seed has the capacity to germinate over a wide range of normal physical environmental factors that include water, oxygen, and appropriate temperature (Finch-Savage & Leubner-Metzger, 2006; Thompson & Ooi, 2013 and references therein). A dormant seed is one that contains a viable embryo but will not germinate under the normal physical conditions that otherwise would be favorable for its germination (Baskin & Baskin, 2004; Hilhorst, 2011). The adaptive significance of seed dormancy is to distribute germination in time and space, so that seedling establishment takes place in circumstances that ensure survival and growth (Fenner & Thompson, 2005; Finch-Savage & Leubner-Metzger, 2006; Heschel et al., 2007).

Plant lineages have independently evolved a variety of mechanisms related to seed dormancy in response to diverse selective pressures (Linkies et al., 2010). Nearly 60% of the species found in tropical rainforests and about 50% of those found in tropical semi-evergreen forests are nondormant. In contrast, more than 70% of savanna seeds are dormant (Baskin & Baskin, 2004). There is no evidence supporting seed dormancy in the Melastomataceae in the Atlantic forest (see Table 1). In the cerrado, however, seed dormancy evolved multiple times in seed-dispersing species during conditions unfavorable for establishment, irrespective of phylogenetic position (Silveira et al., 2012b). Consistently, species fruiting in places and times favorable for seedling establishment produce nondormant seeds (Silveira et al., 2012b). The lack of data on WELS and embryo viability (Hilhorst, 2011) casts some doubt on early and recent reports of dormant seeds in melastomes from rainforests (Ellison et al., 1993; Andrade, 1995; Lopes et al., 2005) and savannas (Pereira-Diniz, 2003; Mendes-Rodrigues et al., 2010).

Seeds of melastomes are physiologically dormant (Baskin et al., 1999; Silveira et al., 2012b). Although there is a layer of lignified cells in the seed coat (Baskin & Baskin, 1998), the seed structure of melastomes does not offer resistance to germination (Cortez & Carmello-Guerreiro, 2008). Further, melastome seeds have fully developed embryos (Forbis et al., 2002) and apparently lack either morphological or morphophysiological dormancies. We adhere to the assertion from Thompson and Ooi (2013) that light is not a dormancy factor, but rather a germination requirement. If photodormancy is considered, then all melastomes produce dormant seeds.

Seed Bank Formation

Melastome seeds are among the most abundant and diverse families in the soil seed bank communities across numerous physiognomies in both cerrado and Atlantic forest (Sassaki et al., 1999; Carreira, 2004; Pereira-Diniz & Ranal, 2006; Medina & Fernandes, 2007). Melastome seeds can be found at several soil depths (Pereira-Diniz & Ranal, 2006) in both dry and wet seasons (Sassaki et al., 1999), which accounts for a significant portion of emergent seedlings. Miconieae and Melastomeae predominate in forest seed banks (Baider et al., 1999), whereas Microlicieae stands out in rupestrian grasslands (Medina & Fernandes, 2007).

Melastome seeds are found in seed banks in degraded areas, secondary growth, and mature forest stands, but the seed density of *Miconia* and *Tibouchina* decreases with increasing forest age (Baider et al., 1999). These species constitute early or pioneer communities, which are essential for the establishment of more shade-tolerant trees and consequent forest regeneration (Baider et al., 1999). Thus, the richness of melastomes in soil seed banks highlights their potential role in ecological restoration.

The typically small-sized seeds of the Melastomataceae may be regarded as the principal factor in high seed longevity, rather than seed dormancy (Thompson et al., 2003). Ease in the burial of smaller seeds would inhibit germination and decrease predation, suggesting a predictable relationship between small seed size and persistence in soil (Milberg et al., 2000; Fenner & Thompson, 2005). Artificially stored melastome seeds demonstrated high longevities (Zaia & Takaki, 1998; Pereira-Diniz, 2003; Carreira, 2004). Melastomes produce large numbers of seeds (more than 1000 fruits/individual) (Galetti & Stotz, 1996; Dalling et al., 1998; F. A. O. Silveira, pers. obs.) in a short period of time (less than two months) and enter tropical seed banks together with other woody pioneer and herbaceous species (Baskin & Baskin, 1998), thus playing an important role in regeneration following disturbance. High seed longevity along with high potential to enter and persist in seed banks and copious fruit production may explain why invasive melastomes such as *Miconia calvescens* DC. and *Clidemia hirta* can be difficult to control (Meyer & Florence, 1996).

Seedling Establishment

Seedling establishment is the most fragile phase in the plant's life cycle. Understanding how seedlings respond to both biotic and abiotic stresses is crucial for the conservation and management of plant populations and for ecological restoration. One would expect remarkable differences in recruitment between cerrado and Atlantic forest species of the Melastomataceae because these habitats provide such contrasting conditions for the establishment phase. Studies on melastome seedling establishment are rare; therefore, the following discussion is based on studies from the rainforests of Central America as well as those few studies conducted for cerrado species.

Early accounts of germination and establishment of woody plants in the cerrado indicate little success of sexual reproduction under laboratory conditions in spite of the high proportion of viable seeds and good germinability (Oliveira, 2008). These initial studies were based on observations that a high proportion of species in the community is able to reproduce vegetatively, suggesting that fire-induced mortality would limit the role of regeneration from seeds (Fig. 11). Here, we discuss how drought, fire, cover effects, and interspecific competition impact seedling establishment in the cerrado.

Water shortages during the dry season limit establishment of seedlings to intervals of sufficiently high soil moisture (Salazar et al., 2011). Root systems of seedling and juvenile plants restrict to upper layers of soil in initial development and therefore lack access to available water from deeper soil layers during the dry season (Goldstein et al., 2008). Melastome seeds may germinate in September, but drought-induced mortality in the early wet season may select for delayed germination until the arrival of consistent rainfall during the mid-rainy season (Pereira-Diniz & Ranal, 2006). High soil evapotranspiration at the onset of the rainy season may prevent water from penetrating the lower soil layers; constant irrigation positively increased seedling establishment of *Miconia albicans* (Hoffmann, 1996). For this species, recruitment begins in December, peaks in February, and decreases as the dry season proceeds (Carreira, 2004). Establishment during the mid-rainy

season is an effective strategy to ensure seedling growth and root elongation, resulting in the typical low shoot to root ratio of cerrado species in central Brazil (Hoffmann & Franco, 2003). The higher biomass allocation to roots allows the plant to access deeper soil layers where moisture remains accessible, even after several months without rains (Goldstein et al., 2008).

Fire may also be selective for melastome seedling establishment during the rainy season. Fire negatively affects sexual reproduction, destroys reproductive structures, decreases size-specific reproductive output, and kills seedlings (Hoffmann, 1998). Forest species are fire-sensitive, whereas most cerrado species resprout after fire (Hoffmann, 2000). Fire-induced mortality is particularly costly for small-seeded species, killing 100% of 2-year-old *Miconia albicans* seedlings (Hoffmann, 1998). Thus, seedling establishment of *M. albicans* and *Clidemia sericea* D. Don. peaks in the second and third year after fire (Miyanishi & Kellman, 1986).

Cover effects on seedling establishment in the Melastomataceae include canopy shading and litter cover. Canopy shading is usually neglected as a limiting factor in the cerrado, but potentially restricts seedling growth during early establishment even in open grasslands, noted particularly for cerrado woodlands (Franco, 2002; Goldstein et al., 2008). The grass layer reduces up to 70% of photosynthetic photon flux densities (Franco, 2002) and is likely to alter R:FR light ratios, hence hampering regeneration from seed. Ground litter modifies conditions on the soil surface by intercepting light, reducing thermal amplitude, releasing nutrients and toxins, and reducing evaporation (Fenner & Thompson, 2005). In woodlands, litter may prevent the establishment of *Miconia*. In open grassland, however, scant litter positively affects establishment by reducing soil temperature and desiccation (Hoffmann, 1996).

Finally, grass root competition for water is critical during the wet season in the cerrado, even though topsoil layers remain wet most of the time. Low shoot to root ratio and biomass allocation to roots (Goldstein et al., 2008) allows roots to reach moist soil layers beyond the grass root zone. Also, the buildup of underground energy reserves facilitates regrowth of aerial biomass after fire or drought (Franco, 2002). We lack information on whether the lower amount of melastome seed reserves would limit seedling root growth, thereby affecting competition with grass roots.

Recruitment in forests drastically differs from that in savannas. The closed rainforest canopy alters light quality and quantity (Zaia & Takaki, 1998), thereby hindering regeneration from photoblastic seeds. The light-requiring melastome seeds accumulate in the seed banks and germination is prevented unless canopy gaps occur. Small-seeded species respond to an irradiance cue for germination, while larger-seeded pioneers respond positively to increasing diel temperature fluctuations (Pearson et al., 2002). Despite low survival success (less than 5%), *Miconia* seedlings are 20-fold more abundant in gaps than in understory, with emergence increasing with gap size (Ellison et al., 1993). Because canopy gaps reduce soil moisture (Ellison et al., 1993), seedling mortality in gap-induced dry soils should select for germination in suitable microsites within the gap. Melastomes preferentially recruit in litter-free microsites (Metcalfe et al., 1998; Dalling & Hubell, 2002) as a thicker litter affects light penetration and reduces the R:FR light ratios to inhibitory levels for germination (Pearson et al., 2003a). Melastome seedlings are unevenly distributed within gaps, known to be frequent in root pit and mound microsites (Ellison et al., 1993). Small-seeded species germinate only in comparatively moist microsites as presented by small canopy gaps, which may reduce the risk of drought-induced mortality (Daws et al., 2008).

Interactions with Seed Pathogens, Predators, and Micorrizhae

Melastome fruit and seed interactions with fungi and seed predators are poorly known, despite their ecological and applied relevance. The available studies indicate a great diversity of pre- and post-dispersal seed predators and pathogens in Neotropical melastomes. At least seven seed-feeder species of *Notiobia* (Carabidae) beetles are associated with fallen fruits of *Bellucia* Neck. ex Raf., *Loreya* DC., and *Miconia* in the Amazon (Paarmann et al., 2002). A recently described species of *Allorhogas* (Hymenoptera: Braconideae) induces galls in 15%–58% fruits of *Conostegia xalapensis* (Bonpl.) D. Don, severely decreasing fruit size and seed number (Chavarría et al., 2009). Two species of *Ditylenchus* (Tylenchida: Anguinidae) induce galls in leaves and fruits of cerrado (Viana et al., 2013) and Atlantic forest (Santos et al., 2012) Melastomataceae (Oliveira et al., 20132). Such nematode galls drain photosynthate, destroy infructescences, or both, affecting plant fitness (Viana et al., 2013; Fig. 1H). Their widespread occurrence in the Miconieae (Oliveira et al., 2013) suggests unnoticed negative consequences of nematode-induced galls in the reproduction of native species (Santos et al., 2012; Viana et al., 2013). The overall effect of seed pathogens and predators in recruitment of melastomes is currently unknown, but antagonists have been suggested as

Table 2. Germinability (%) of *Comolia sertularia* (DC.) Triana and *Microlicia tetrasticha* Cogn. seeds under different light and temperature conditions. Four replicates of 25 seeds for each species were set to germinate under conditions of a 12-hour photoperiod (12 hours of light, followed by 12 hours of darkness) and continuous dark (24 hours). Temperatures were held constant at 15°C, 20°C, 25°C, and 30°C, respectively, for 30 consecutive days. Dashes (—) indicate that data were not available. Original data by the authors.

		Germinability (%)							
		15°C		20°C		25°C		30°C	
Species	Year of collection	Light	Dark	Light	Dark	Light	Dark	Light	Dark
C. sertularia	2001	0	0	1	0	3	2	—	—
C. sertularia	2002	0	0	1	0	0	0	1	0
M. tetrasticha	2001	2	0	0	0	0	0	—	—

agents of biological control of invasive melastomes (Seixas et al., 2004; Oliveira et al., 2013).

Fungal and oomyceteous pathogens are major causes of seed mortality for some *Miconia* (Dalling et al., 1998) and may decrease recruitment from seed banks. On the other hand, the occurrence of mycorrizhae in the Melastomataceae may be underestimated and their potential in increasing establishment has been overlooked (Metcalfe et al., 1998; Urcelay et al., 2005; Matias et al., 2009). Nothing is yet known about the role of fungal endophytes in seed and seedling ecology of melastomes.

Seed Ecology of Melastomes in a Changing World

effects of global change

Global climate change effects on germination are speculative since responses are species specific (Fenner & Thompson, 2005), and, thus, the following discussion should be viewed with caution. Regeneration from seed is often expected to benefit from climate warming, perhaps because studies focused on colder regions of the globe (Fenner & Thompson, 2005). Although no study tested the effects of elevated CO_2 and temperature on melastome germination, we predict a negative impact of temperature raise on regeneration from seed banks because melastome germination is disfavored at high temperatures (Tables 1 and 3, Silveira, 2011).

Data forecast a 10%–20% reduction in precipitation in both savannas and rainforests during the dry season (IPCC, 2007). Conversion of cerrado to grasslands increases mean surface air temperature and the frequency of dry periods within the wet season (Hoffmann & Jackson, 2000), changes that could be damaging to melastome seedlings. Despite the effects of changes in precipitation being difficult to predict (Fenner & Thompson, 2005), they will likely constrain melastome recruitment through a predicted shortened rainy season and decreased soil moisture (see Table 3). The intensification of fire frequency may further impact recruitment. Enlarged fire seasons can be detrimental to ecotone-colonizing plants at cerrado–forest boundaries.

Finally, climate change may indirectly disrupt fruit–frugivore interactions by simultaneously reduc-

Table 3. Predicted effects of ongoing human activities on the life cycle transitions of Neotropical Melastomataceae. Plus sign (+) indicates beneficial effects; minus sign (–) reflects deleterious effects; zero (0) indicates neutral, and a question mark (?) indicates unpredictable response.

	CO_2 increase	Temperature rise	Fire increase	Precipitation decrease	Habitat fragmentation
Seed production	?	?	–	–	?
Bird dispersal distance	0	?	0	–	–
Ant dispersal distance	0	?	0	0	–
Seed rain	0	?	0	–	?
Wind dispersal	0	0	0	0	?
Ant–fruit interactions	0	0	–	0	–
Germinability	?	–	–	–	+
Germination time	?	?	–	–	0
Seed bank dynamics	?	–	–	–	+
Seedling establishment	?	–	–	–	–
Seedling herbivory	–	–	0	0	–

ing bird distribution range and promoting frugivore extinction (see Table 3). One estimate predicts that nearly 80% of Amazon manakins would lose their habitable area, and 20% of cerrado manakin species would face extinction under future climate changes (Anciães & Peterson, 2006).

Effects of Habitat Fragmentation

The increasing and unprecedented deforestation level is creating a landscape of edge-dominated forests where edges are more illuminated, desiccated, and wind-exposed than forest interior. Microclimatic alterations change the structure of forest communities, driving the forest fragments toward early-successional conditions (Tabarelli et al., 2008). Pioneer-dominated plant assemblages in forest edges are markedly different in terms of tree species richness and proportion of pioneer and large-seeded species compared to the forest interior (Silva et al., 2007; Santos et al., 2008). A dramatic shift in the plant community in the Atlantic forest toward small-fruited and capsule-bearing species (Silva & Tabarelli, 2000) results from forest fragmentation, selective logging, and hunting pressure, leading to local extinction of large-fruited trees and the movement of large fruit-eating vertebrates out of the region. The apparent success of small-seeded species in disturbed habitats must be assessed in the long term to accurately determine how the melastomes will respond to fragmentation in defaunated areas.

Bird response to fragmentation and consequences for melastome recruitment

Mechanisms determining bird distribution in edges versus forest interior include changes in microclimate, distribution of suitable habitats, parasites and predators, and resource-driven mechanisms (Restrepo & Goméz, 1998). Fragmentation changes bird abundance, richness, and behavior (e.g., movement patterns and fruit consumption), and no general pattern of bird responses to fragmentation emerges because anthropogenic disturbances influence the distribution of understory birds in complex ways (Restrepo & Goméz, 1998; Restrepo et al., 1999; Galetti et al., 2003; Martensen et al., 2008). The result is an altered bird community structure and composition in fragmented areas compared to pristine areas (Restrepo & Goméz, 1998).

Few studies have looked at the fragmentation effects on seed rain, but birds may be unresponsive to changes in fruit abundance in edges versus forest interior (Levey, 1990; Restrepo et al., 1999). Changes in the distribution and survival of frugivores suggest that seed delivery may be reduced in fragments, leading to changes in fruit removal rates as well as the structure and location of edges over time (Restrepo & Goméz, 1998; Galetti et al., 2003). Theoretically, the demography of generalist bird-dispersed small-seeded species, such as Melastomataceae and Rubiaceae, can be affected by fragmentation (Galetti et al., 2003). Because melastome species account for nearly 20% of fruit–frugivore interactions in the forest edge, secondary growth, and also in the canopy and understory of mature Atlantic forests (Silva et al., 2002), the impact should be noteworthy.

Negative effects of fragmentation on fruit removal are not unequivocal (Restrepo et al., 1999). The probability of fruit consumption is lower in the interior than at the edge and in small rather than in large fragments (Galetti et al., 2003). Conversely, higher seed rain of small-sized seeds at the northeastern Atlantic forest edge explains continuous recruitment (Melo et al., 2006). In Central American melastomes, removal rates are higher in young-secondary forest than in old-growth forest regardless of where plants grew. This was associated with higher sugar concentration in berries from young-secondary forest compared to those in old-growth forest species (Lumpkin & Boyle, 2009). Fragmentation effects on seed rain are complex perhaps because of diversity of plant functional types in species-rich tropical forests, but decreased seed dispersal does not necessarily lead to lower recruitment (Valdivia & Simonetti, 2007).

Large fruit–frugivore networks in the Atlantic forest may provide resilience to disturbance (Silva et al., 2007). Forest fragmentation is thought to favor small-seeded species (Silva & Tabarelli, 2000), and, thus, melastomes may not be negatively affected in the short term. Small-seeded plant species are favored because of the dominance of small, habitat-generalist birds. Most of the melastome seed dispersers do well in degraded areas (Pizo, 2007), and disruption of fruit–frugivore mutualism may have only minor effects. Bird distribution is edge-age dependent, so it can be reasoned that time-lag responses may have gone undetected. Additionally, increased fire frequency will likely prevent seedling establishment in forest edges.

Ant response to fragmentation and consequences for melastome recruitment

Ants can be relevant fruit rescuers in sites impoverished of vertebrate dispersal assemblages, and in fragmented or heavily hunted habitats (Christianini & Oliveira, 2009). Therefore, as habitat loss and fragmentation reduce abundance and richness of frugivorous birds, the relative importance

Table 4. The advantages and disadvantages of using Melastomataceae in the most recommended ecological restoration techniques (see text for references to the exemplar recommended techniques).

Restoration technique	Advantage	Disadvantage
Fire protection	a fire-free environment is likely to increase recruitment because of seed and seedling fire sensitivity	may be implicated in problems with farmers, requiring pre-action, social mobilization
Perching	profuse berry production is attractive for a wide range of taxonomic vertebrates, nucleation enhancement, and low cost of implementation	none
Seed rain management	large production of long-lived seeds, low cost for seed rain collection	no control of final seedling number
Seed sowing	copious seed production and low cost for seed collection, handling, and sowing	low seedling recruitment; no control of final seedling number
Litter and soil seed bank management	ubiquity and abundance of melastome seeds in tropical seed banks	may decrease regeneration in nearby fragments
Seedling resprout	very limited technique	melastome studied to date are obligate seeders following disturbance
Seedling transplanting	high seed production and rapid early seedling growth, which ensures control of final seedling number	relatively elevated costs for seedling production

of secondary dispersal by ants increases. Leaf-cutting ants (*Atta* and *Acromyrmex*), the major seed-harvesting ants (Dalling & Wirth, 1998; Leal & Oliveira, 1998; Christianini & Oliveira, 2009; Lima et al., 2013), appear to benefit from fragmentation. Colonies of *Atta sexdens* L. and *Atta cephalotes* L. are more frequently found in forest edges and second-growth forest regeneration patches than in the forest interior as a consequence of shifts in both bottom-up and top-down control (Silva et al., 2009). However, increased herbivory by leaf-cutting ants in the forest edge has also been documented (Urbas et al., 2007; Silva et al., 2009). In highly disturbed sites, colony density increases, but foraging areas of colonies is dramatically reduced compared to forest interiors (Urbas et al., 2007), suggesting that fragmentation indirectly reduces ant dispersal distance (Table 3). Seed harvesting by ants in disturbed areas would restrict seed dispersal to short distances, promote seed clumping, and reduce seedling survival beneath parents, overcoming any positive benefit plants would derive from seed dispersal by ants (Guimarães & Cogni, 2002; Silva et al., 2007).

IMPLICATIONS FOR RESTORATION

Ecological restoration is a high-priority issue in the conservation agenda for Neotropical hotspots. Here, we discuss how the ecology of melastomes can assist seed- and seedling-based restoration approaches (Rodrigues et al., 2009). First, the small-sized fruits of melastomes contain a high number of seeds and are produced year round. This has three key implications for restoration (Table 4): (1) high seed availability does not prevent seedling density improvement and enrichment through seed sowing; (2) berries are attractive to a diverse community of generalist frugivores that deliver seeds from other species to nucleated sites; and (3) transplanted berry-fruited melastomes can surrogate the use of artificial perches and act as stepping stones in fragmented areas.

Second, melastomes are abundant and diverse in tropical soil seed banks (see Seed Bank Formation), allowing transference of litter and soil seed bank from nearby conserved sites. Finally, melastome seedlings have high growth rates (Carreira & Zaidan, 2003; Ranieri et al., 2005), increasing soil coverage and conservation. The inoculation of mycorrhizae and *Rhizobium* promotes increased survival and growth of *Tibouchina heteromalla* (Matias et al., 2009), and can be an alternative for sapling limitation (Table 4).

Melastomataceae are able to colonize degraded areas and create suitable conditions for the establishment of secondary and late-successional species, even in areas with soils contaminated with heavy metals (Jacobi et al., 2007; Rodrigues & Silveira, 2013). They also interact with a wide diversity of pollinators and seed dispersers, and can assist in restoring ecological interactions and ecosystem services. However, melastomes are sensitive to fire and may have a limited role in forest restoration during advanced successional stages. We hope our efforts encourage their use in future ecological restoration programs.

Conclusions

Current data reveal the following findings: (1) capsules are dispersed during the dry–wet transition season, whereas berries are produced year round; (2) tanagers, manakins, and thrushes are the major seed dispersers, but a broad range of bird species also are important in providing seed cleaning and in transporting fruits away from parent plants; (3) ants are dominant secondary seed dispersers, with important benefits arising from their interaction with berries; (4) the small-sized seeds are light demanding, long lived, and accumulate in soil seed banks; (5) physiological dormancy evolved in the cerrado but not in the Atlantic forest; (6) litter abundance, gap size, and within-gap microsite can affect regeneration from seed in forests, whereas fire and drought are determinant for establishment in the cerrado; and (7) fruit traits of Melastomataceae can assist seed-based restoration ecology techniques.

Literature Cited

Alves, M. A. S., P. D. Ritter, R. D. Antonini & E. M. Almeida. 2008. Two thrush species as dispersers of *Miconia prasina* (Sw.) DC. (Melastomataceae): An experimental approach. Brazil. J. Biol. 68: 397–401.

Alves-Costa, C. P. & P. C. Eterovick. 2007. Seed dispersal services by coatis (*Nasua nasua*, Procyonidae) and their redundancy with other frugivores in southeastern Brazil. Acta Oecol. 32: 77–92.

Amaral, L. I. V. & M. T. S. Paulilo. 1992. Efeito da luz, temperatura, reguladores de crescimento e nitrato de potássio na germinação de *Miconia cinnamomifolia* (DC.) Naudim. Insula 21: 59–86.

Anciães, M. & A. T. Peterson. 2006. Climate change effects on Neotropical manakin diversity based on ecological niche modeling. The Condor 108: 778–791.

Andrade, A. C. S. 1995. Efeito da luz e da temperatura na germinação de *Leandra breviflora* Cogn., *Tibouchina benthamiana* Cogn., *Tibouchina grandifolia* Cogn. e *Tibouchina moricandiana* (DC.) Baill. (Melastomataceae). Revista Brasil. Sementes 17: 29–35.

Baider, C., M. Tabarelli & W. Mantovani. 1999. The soil seed bank of a tropical montane forest, Brazil. Revista Brasil. Biol. 59: 319–328.

Barbosa, J. M., L. M. Barbosa, M. M. Pinto & I. B. Aguiar. 1988. Efeito do substrato, temperatura e luminosidade na germinação de sementes de quaresmeira. Revista Brasil. Sementes 10: 69–77.

Baskin, C. C. & J. M. Baskin. 1998. Seeds: Ecology, Biogeography and Evolution of Dormancy and Germination. Academic Press, San Diego.

Baskin, C. C. & J. M. Baskin. 2007. A revision of Martin's seed classification system, with particular reference to his dwarf-seed type. Seed Sci. Res. 17: 11–20.

Baskin, C. C., J. M. Baskin & E. W. Chester. 1999. Seed dormancy and germination in *Rhexia mariana* var. *interior* (Melastomataceae) and eco-evolutionary implications. Canad. J. Bot. 77: 488–493.

Baskin, J. M. & C. C. Baskin. 2004. A classification system for seed dormancy. Seed Sci. Res. 14: 1–16.

Baumgratz, J. F. A. 1985. Morfologia dos frutos e sementes de Melastomataceae brasileiras. Arch. Jard. Bot. Rio de Janeiro 27: 113–155.

Baumgratz, J. F. A., M. L. D. R. Souza, D. C. Carraça & B. A. Abbas. 2006. Melastomataceae na reserva biológica de Poço das Antas, Silva Jardim, Rio de Janeiro, Brasil: Aspectos florísticos e taxonômicos. Rodriguésia 57: 591–646.

Blendinger, P. G., B. A. Loiselle & J. G. Blake. 2008. Crop size, plant aggregation, and microhabitat type affect fruit removal by birds from individual melastome plants in the Upper Amazon. Oecologia 158: 273–283.

Carreira, R. C. 2004. Germinação de sementes de *Miconia albicans* (Sw.) Triana e *M. rubiginosa* (Bonpl.) DC., Melastomataceae, do cerrado de Mogi Guaçu, SP. Ph.D. Dissertation, Instituto de Botânica, São Paulo.

Carreira, R. C. & L. B. P. Zaidan. 2003. Estabelecimento e crescimento inicial de *Miconia albicans* (Sw.) Triana e *Schizocentron elegans* Meissn., sob fotoperíodos controlados. Hoehnea 30: 155–161.

Carreira, R. C. & L. B. P. Zaidan. 2007. Germinação de sementes de espécies de Melastomataceae de cerrado sob condições controladas de luz e temperatura. Hoehnea 34: 261–269.

Casal, J. J. & R. Sánchez. 1998. Phytochromes and seed germination. Seed Sci. Res. 8: 317–329.

Cavalcanti, D. R. & M. Tabarelli. 2004. Distribuição das plantas amazônico-nordestinas no centro de endemismo Pernambuco: Brejos de altitude vs. florestas de terras baixas. Pp. 285–296 *in* K. C. Pôrto, J. J. P. Cabral & M. Tabarelli (editors), Brejos de Altitude em Pernambuco e Paraíba: História Natural, Ecologia e Conservação. Ministério do Meio Ambiente, Brasilia.

Chavarría, L., P. Hanson, P. Marsh & S. Shaw. 2009. A phytophagous braconid, *Allorhogas conostegia* sp. nov. (Hymenoptera: Braconidae), in the fruits of *Conostegia xalapensis* (Bonpl.) D. Don (Melastomataceae). J. Nat. Hist. 43: 2677–2689.

Christianini, A. V. & P. S. Oliveira. 2009. The relevance of ants as seed rescuers of a primarily bird-dispersed tree in the Neotropical cerrado savanna. Oecologia 160: 735–745.

Clausing, G. & S. S. Renner. 2001. Molecular phylogenetics of Melastomataceae and Memecylaceae: Implications for character evolution. Amer. J. Bot. 88: 486–498.

Clausing, G., K. Meyer & S. S. Renner. 2000. Correlations among fruit traits and evolution of different fruits within Melastomataceae. Bot. J. Linn. Soc. 133: 303–326.

Cortez, P. A. & S. M. Carmello-Guerreiro. 2008. Ontogeny and structure of the pericarp and the seed coat of *Miconia albicans* (Sw.) Triana (Melastomataceae) from "cerrado", Brazil. Revista Brasil. Bot. 31: 71–79.

Dalling, J. W. & R. Wirth. 1998. Dispersal of *Miconia argentea* seeds by the leaf-cutting ant *Atta colombica*. J. Trop. Ecol. 14: 705–710.

Dalling, J. W. & S. P. Hubbell. 2002. Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. J. Ecol. 90: 557–568.

Dalling, J. W., S. P. Hubbell & K. Silvera. 1998. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. J. Ecol. 86: 674–689.

Daws, M. I., L. M. Crabtree, J. W. Dalling, C. E. Mullins & D. Burslem. 2008. Germination responses to water potential in Neotropical pioneers suggest large-seeded species take more risks. Ann. Bot. 102: 945–951.

de Figueiredo, R. A. & C. A. Longatti. 1997. Ecological aspects of the dispersal of a Melastomataceae by marmosets and howler monkeys (Primates: Platyrrhini) in a semideciduous forest of southeastern Brazil. Rev. d'Ecologie 52: 3–8.

Donohue, K., R. R. Casas, L. Burghardt, K. Kovach & C. G. Willis. 2010. Germination, postgermination adaptation, and species ecological ranges. Ann. Rev. Ecol. Evol. Syst. 41: 293–319.

Elisson, A. M., J. S. Denslow, B. A. Loiselle & D. Brenés M. 1993. Seed and seedling ecology of neotropical Melastomataceae. Ecology 74: 1733–1749.

Farnsworth, E. 2000. The ecology and physiology of viviparous and recalcitrant seeds. Ann. Rev. Ecol. Evol. Syst. 31: 107–138.

Fenner, M. & K. Thompson. 2005. The Ecology of Seeds. University Press, Cambridge.

Finch-Savage, W. E. & G. Leubner-Metzger. 2006. Seed dormancy and the control of germination. New Phytol. 171: 501–523.

Forbis, T. A., S. K. Floyd & A. de Queiroz. 2002. The evolution of embryo size in angiosperms and other seed plants: Implications for the evolution of seed dormancy. Evolution 56: 2112–2125.

Franco, A. C. 2002. Ecophysiology of woody plants. Pp. 178–197 *in* P. S. Oliveira & R. J. Marquis (editors), The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna. Columbia University Press, New York.

Fritsch, P. W., F. Almeda, S. S. Renner, A. B. Martins & B. C. Cruz. 2004. Phylogeny and circumscription of the near-endemic Brazilian tribe Microlicieae (Melastomataceae). Amer. J. Bot. 91: 1105–1114.

Galetti, M. & D. Stotz. 1996. *Miconia hypoleuca* (Melastomataceae) como espécie-chave para aves frugívoras no sudeste do Brasil. Revista Brasil. Biol. 56: 435–439.

Galetti, M., C. Costa & E. Cazetta. 2003. Effects of forest fragmentation, anthropogenic edges and fruit color on the consumption of ornithochoric fruits. Biol. Conservation 111: 269–293.

Garcia, L. C., F. V. Barros & J. P. Lemos-Filho. 2006. Comportamento germinativo de duas espécies de canga ferrífera: *Baccharis retusa* DC. (Asteraceae) e *Tibouchina multiflora* Cogn. (Melastomataceae). Acta Bot. Bras. 20: 443–448.

Garcia, L. C., F. V. Barros & J. P. Lemos-Filho. 2009. Fructification phenology as an important tool in the recovery of iron mining areas in Minas Gerais, Brazil. J. Biol. 69: 887–893.

Garcia, Q. S., J. L. P. Rezende & L. M. S. Aguiar. 2000. Seed dispersal by bats in a disturbed area of southeastern Brazil. Revista Biol. Trop. 48: 125–128.

Godoi, S. & M. Takaki. 2007. Seed germination in *Miconia theaezans* (Bonpl.) Cogniaux (Melastomataceae). Brazil. Arch. Biol. Technol. 50: 571–578.

Godoi, S., A. Grandis & M. Takaki. 2009. A germinação de sementes de *Miconia theaezans* (Bonpl.) Cogniaux (Melastomataceae) é controlada pelo fitocromo. Naturalia 32: 13–22.

Goldenberg, R. & G. J. Shepherd. 1998. Studies on the reproductive biology of Melastomataceae in "cerrado" vegetation. Pl. Syst. Evol. 211: 13–29.

Goldenberg, R., D. S. Penneys, F. Almeda, W. S. Judd & F. A. Michelangeli. 2008. Phylogeny of *Miconia* (Melastomataceae): Patterns of stamen diversification in a megadiverse Neotropical genus. Int. J. Pl. Sci. 169: 963–979.

Goldstein, G., F. C. Meinzer, S. J. Bucci, F. G. Scholz, A. C. Franco & W. A. Hoffmann. 2008. Water economy of Neotropical savanna trees: Six paradigms revisited. Tree Physiol. 28: 395–404.

Gomes, V. S. D., M. C. R. Correia, H. A. de Lima & M. A. S. Alves. 2008. Potential role of frugivorous birds (Passeriformes) on seed dispersal of six plant species in a restinga habitat, southeastern Brazil. Revista Biol. Trop. 56: 205–216.

Gridi-Papp, C. O., M. Gridi-Papp & W. R. Silva. 2004. Differential fruit consumption of two Melastomataceae by birds in Serra da Mantiqueira, southeastern Brazil. Ararajuba 12: 5–10.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: The importance of the regeneration niche. Biol. Rev. 52: 107–145.

Guimarães Jr., P. R. & R. Cogni. 2002. Seed cleaning of *Cupania vernalis* (Sapindaceae) by ants: Edge effects in a highland forest in southeast Brazil. J. Trop. Ecol. 18: 303–307.

Guimarães Jr., P. R., M. Galetti & P. Jordano. 2008. Seed dispersal anachronisms: Rethinking the fruits extinct megafauna ate. PLoS ONE 3: e1745

Heschel, M. S., J. Selby, C. Butler, G. C. Whitelam, R. A. Sharrock & K. Donohue. 2007. A new role for phytochromes in temperature-dependent germination. New Phytol. 174: 735–741.

Hilhorst, H. W. M. 2011. Standardizing seed dormancy research. Pp. 43–52 *in* A. R. Kermode (editor), Seed Dormancy: Methods and Protocols. Springer, New York.

Hoffmann, W. 1996. The effects of fire and cover on seedling establishment in a neotropical savanna. J. Ecol. 84: 383–393.

Hoffmann, W. 1998. Post-burn reproduction of woody plants in a neotropical savanna: The relative importance of sexual and vegetative reproduction. J. Appl. Ecol. 35: 422–433.

Hoffmann, W. 2000. Post-establishment seedling success in the Brazilian cerrado: A comparison of savanna and forest species. Biotropica 32: 62–69.

Hoffmann, W. & R. B. Jackson. 2000. Vegetation-climate feedbacks in the conversion of tropical savanna to grassland. J. Climate 13: 1593–1602.

Hoffmann, W. & A. C. Franco. 2003. Comparative growth analysis of tropical forest and savanna woody plants using phylogenetically independent contrasts. J. Ecol. 91: 475–484.

IPCC Climate Change. 2007. Summary for policymakers. Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Jacobi, C. M., F. F. Carmo, R. C. Vincent & J. R. Stehmann. 2007. Plant communities on ironstone outcrops: A diverse and endangered Brazilian ecosystem. Biodivers. & Conservation 16: 2185–2200.

Kessler-Rios, M. M. & G. H. Kattan. 2012. Fruits of Melastomataceae: Phenology in Andean forest and role as food sources for birds. J. Trop. Ecol. 28: 11–21.

Klink, C. A. & R. Machado. 2005. Conservation of the Brazilian cerrado. Conservation Biol. 19: 707–713.

Lapenta, M. J. & P. Procópio-de-Oliveira. 2008. Some aspects of seed dispersal effectiveness of golden lion tamarins (*Leontopithecus rosalia*) in a Brazilian Atlantic forest. Trop. Conservation Sci. 1: 122–139.

Leal, I. R. & P. S. Oliveira. 1998. Interactions between fungus growing ants (Attini), fruits and seeds in cerrado vegetation in southeast Brazil. Biotropica 30: 170–178.

Lessa, L. G. & F. N. Costa. 2009. Food habits and seed dispersal by *Thrichomys apereoides* (Rodentia, Echimyidae) in a Brazilian cerrado reserve. Mastozoología Neotropical 16: 459–463.

Lessa, L. G. & F. N. Costa. 2010. Diet and seed dispersal by five marsupials (Didelphimorphia: Didelphidae) in a Brazilian cerrado reserve. Mammalian Biol. 75: 10–16.

Levey, D. J. 1990. Habitat-dependent fruiting behaviour of an understorey tree, *Miconia centrodesma*, and tropical treefall gaps as keystone habitats for frugivores in Costa Rica. J. Trop. Ecol. 6: 409–420.

Lima, M. H. C., E. G. Oliveira & F. A. O. Silveira. 2013. Interactions between ants and non-myrmecochorous fruits in species of *Miconia* (Melastomataceae) in a Neotropical savanna. Biotropica 45: 217–233.

Linnebjerg, J. F., D. M. Hansen & J. O. Olesen. 2009. Gut passage effect of the introduced red-whiskered bulbul (*Pycnonotus jocosus*) on germination of invasive plant species in Mauritius. Austral Ecol. 34: 272–277.

Loiselle, B. A. & J. G. Blake. 1999. Dispersal of melastome seeds by fruit-eating birds of tropical forest understory. Ecology 80: 330–336.

Lopes, J. C. & A. S. Soares. 2006. Estudo da maturação de sementes de carvalho vermelho (*Miconia cinnamomifolia* (DC.) Naud). Ci. Agrotécnol. 30: 623–628.

Lopes, J. C., P. C. Dias & M. D. Pereira. 2005. Maturação fisiológica de sementes de quaresmeira. Pesq. Agropecu. Brasil. 40: 811–816.

Lumpkin, H. & W. A. Boyle. 2009. Effects of forest age on fruit composition and removal in tropical bird-dispersed understorey trees. J. Trop. Ecol. 25: 515–522.

Macedo, R. H. F. 2002. The avifauna: Ecology, biogeography, and behavior. Pp. 242–265 *in* P. S. Oliveira & R. J. Marquis (editors), The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna. Columbia University Press, New York.

Magnusson, W. E. & T. M. Sanaiotti. 1987. Dispersal of *Miconia* seeds by the rat *Bolomys lasiurus*. J. Trop. Ecol. 3: 277–278.

Manhães, M. A., L. C. S. Assis & R. M. Castro. 2003. Frugivoria e dispersão de sementes de *Miconia urophylla* (Melastomataceae) por aves em um fragmento de Mata Atlântica secundária em Juiz de Fora, Minas Gerais, Brasil. Ararajuba 11: 173–180.

Mantovani, M., A. R. Ruschel, M. S. Reis, A. Puchalski & R. O. Nodari. 2003. Fenologia reprodutiva de espécies arbóreas em uma formação secundária da floresta Atlântica. Rev. Arv. 27: 451–458.

Marcondes-Machado, L. O. 2002. Comportamento alimentar de aves em *Miconia rubiginosa* (Melastomataceae) em fragmento de cerrado, São Paulo. Iheringia, Série Zool. 92: 97–100.

Martensen, A. C., R. G. Pimental & J. P. Metzger. 2008. Relative effects of fragment size and connectivity on bird community in the Atlantic rainforest: Implications for conservation. Biol. Conservation 141: 2184–2192.

Maruyama, P. K., E. Alves-Silva & C. Melo. 2007. Oferta qualitativa e quantitativa de frutos em espécies ornitocóricas do gênero *Miconia* (Melastomataceae). Revista Brasil. Bioci. 5: 672–674.

Matias, S. R., M. C. Pagano, F. C. Muzzi, A. C. Oliveira, A. A. Carneiro, S. N. Horta & M. R. M. Scotti. 2009. Effect of rhizobia, mycorrhizal fungi and phosphate-solubilizing microorganisms in the rhizosphere of native plants used to recover an iron ore area in Brazil. Eur. J. Soil Biol. 45: 259–266.

McKey, D. 1975. The ecology of coevolved seed dispersal systems. Pp. 159–191 *in* L. E. Gilbert & P. H. Raven (editors), Coevolution of Animals and Plants, University of Texas Press, Austin.

Medina, B. M. O. & G. W. Fernandes. 2007. The potential of natural regeneration of rocky outcrop vegetation on rupestrian field soils in "Sierra do Cipó", Brazil. Revista Brasil. Bot. 30: 665–678.

Melo, F., R. Dirzo & M. Tabarelli. 2006. Biased seed rain in forest edges: Evidence from the Brazilian Atlantic forest. Biol. Conservation 132: 50–60.

Mendes-Rodrigues, C. & P. E. Oliveira. 2012. Polyembryony in Melastomataceae from the Brazilian Cerrado: Multiple embryos in a small world. Pl. Biol. 14: 845–853.

Mendes-Rodrigues, C., F. P. Araújo, C. Barbosa-Souza, V. Barbosa-Souza, M. A. Ranal, D. G. Santana & P. E. Oliveira. 2010. Multiple dormancy and maternal effect on *Miconia ferruginata* (Melastomataceae) seed germination, Serra de Caldas Novas, Goiás, Brazil. Revista Brasil. Bot. 33: 93–105.

Mendonça, M. P. & L. V. Lins (organizers). 2000. Lista vermelha das espécies ameaçadas de extinção da flora de Minas Gerais. Fundação Biodiversitas, Fundação Zoo-Botânica de Belo Horizonte, Belo Horizonte.

Mendonça, R. C., J. M. Felfili, B. M. T. Walter, M. C. Silva, Jr., A. V. Rezende, T. S. Filgueiras, P. E. Nogueira & C. W. Fagg. 2008. Flora vascular do bioma cerrado: Checklist com 12.356 espécies. Pp. 421–1279 *in* S. M. Sano, S. P. Almeida & J. F. Ribeiro (editors), Cerrado: Ecologia e Flora. Embrapa Cerrados, Brasília.

Metcalfe, D. J., P. J. Grubb & I. M. Turner. 1998. The ecology of very small-seeded shade-tolerant trees and shrubs in lowland rainforest in Singapore. Pl. Ecol. 134: 131–149.

Meyer, J-Y. & J. Florence. 1996. Tahiti's native flora endangered by the invasion of *Miconia calvescens* DC. (Melastomataceae). J Biogeogr. 23: 775–781.

Michelangeli, F. A. 2005. *Tococa* (Melastomataceae). Fl. Neotrop. 98: 1–114.

Michelangeli, F. A., P. J. F. Guimarães, D. S. Penneys, F. Almeda & R. Kriebel. 2013. Phylogenetic relationships and distribution of New World Melastomeae (Melastomataceae). Bot. J. Linn. Soc. 171: 38–60.

Milberg, P., L. Andersson & K. Thompson. 2000. Large-seeded species are less dependent on light for germination than small-seeded ones. Seed Sci. Res. 10: 99–104.

Miyanishi, K. & M. Kellman. 1986. The role of fire in recruitment of two Neotropical savanna shrubs, *Miconia albicans* and *Clidemia sericea*. Biotropica 18: 224–230.

Montoro, G. R. & M. L. Santos. 2007. Fenologia e biologia reprodutiva de *Tibouchina papyrus* (Pohl) Toledo no Parque Estadual da Serra dos Pirineus, Goiás. Revista Biol. Neotrop. 4: 21–29.

Morellato, L. P. C. & C. F. B. Haddad. 2000. The Brazilian Atlantic forest: Diversity, ecology and conservation. Biotropica 32: 786–792.

Morellato, L. P. C., D. C. Talora, A. Takahashi, C. C. Bencke, E. C. Romera & V. B. Zipparro. 2000. Phenology of Atlantic rainforest trees: A comparative study. Biotropica 32: 811–823.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Fonseca & J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Oliveira, P. E. A. M. 2008. Fenologia e biologia reprodutiva das espécies do cerrado. Pp. 273–290 *in* S. M. Sano, S. P. Almeida & J. F. Ribeiro (editors), Cerrado: Ecologia e Flora. Embrapa Cerrados, Brasília.

Oliveira, R. D. L., A. M. Santin, D. J. Seni, A. Dietrich, L. A. Salazar, S. A. Subbotin, M. Mundo-Ocampo, R. Goldenberg & R. W. Barreto. 2013. *Ditylenchus gallaeformans* sp. n. (Tylenchida: Anguinidae) a neotropical nematode with biocontrol potential against weedy Melastomataceae. Nematology 15: 179–196.

Oliveira-Filho, A. T. & M. A. L. Fontes. 2000. Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and the influence of climate. Biotropica 32: 793–810.

Oliveira-Filho, A. T. & J. A. Ratter. 2002. Vegetation physiognomies and woody flora of the cerrado biome. Pp. 91–120 *in* P. S. Oliveira & R. J. Marquis (editors), The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna. Columbia University Press, New York.

Paarmann, W., B. Gutzmann, P. Stumpe, H. Bolte, S. Kiippers, K. Holzkamp & C. Niers. 2002. The structure of ground beetle assemblages (Coleoptera: Carabidae) at fruit falls of Melastomataceae trees in a Brazilian Terra Firme Rainforest. Biotropica 34: 368–375.

Pearson, T. R. H., D. Burslem, C. E. Mullins & J. W. Dalling. 2002. Germination ecology of Neotropical pioneers: Interacting effects of environmental conditions and seed size. Ecology 83: 2798–2807.

Pearson, T. R. H., D. Burslem, C. E. Mullins & J. W. Dalling. 2003a. Functional significance of photoblastic germination in Neotropical pioneer trees: A seed's eye view. Funct. Ecol. 17: 394–402.

Pearson, T. R. H., D. Burslem, R. E. Goeriz & J. W. Dalling. 2003b. Regeneration niche partitioning in Neotropical pioneers: Effects of gap size, seasonal drought and herbivory on growth and survival. Oecologia 137: 456–465.

Pereira, T. S. & W. Mantovani. 2001. Maturação e dispersão de *Miconia cinnamomifolia* (DC.) Naud. na Reserva Biológica de Poço das Antas, município de Silva Jardim, RJ, Brasil. Acta Bot. Brasil. 15: 335–348.

Pereira-Diniz, S. G. 2003. Ecofisiologia da germinação de sementes de *Clidemia hirta* (L.) D. Don (Melastomataceae). M.S. Thesis, Universidade Federal de Uberlândia, Uberlândia.

Pereira-Diniz, S. G. & M. A. Ranal. 2006. Germinable soil seed bank of a gallery forest in Brazilian cerrado. Pl. Ecol. 183: 337–348.

Pizo, M. A. 2007. Frugivory by birds in degraded areas of Brazil. Pp. 615–627 *in* A. J. Dennis, E. W. Schupp, R. J. Green & D. A. Westcott (editors), Seed Dispersal: Theory and Its Application in a Changing World. CABI Publishing, Oxfordshire.

Pizo, M. A. & P. S. Oliveira. 2000. The use of fruits and seeds by ants in the Atlantic forest of southeast Brazil. Biotropica 32: 851–861.

Pizo, M. A. & L. P. C. Morellato. 2002. A new rain-operated seed dispersal mechanism in *Bertolonia mosenii* (Melastomataceae), a neotropical rainforest herb. Amer. J. Bot. 89: 169–171.

Poulin, B., S. J. Wright, G. Lefebvre & O. Calderón. 1999. Interspecific synchrony and asynchrony in the fruiting phenologies of congeneric bird-dispersed plants in Panama. J. Trop. Ecol. 15: 213–227.

Ranieri, B. D., T. C. Lana, D. Negreiros, L. M. Araújo & G. W. Fernandes. 2003. Germinação de sementes de *Lavoisiera cordata* e *Lavoisiera francavillana* (Melastomataceae), espécies simpátricas da Serra do Cipó, Brasil. Acta Bot. Brasil. 17: 523–530.

Ranieri, B. D., T. C. Lana, L. Gluck & G. W. Fernandes. 2005. Early growth, architecture and flowering of *Lavoisiera francavillana* (Melastomataceae), a threatened Brazilian shrub with ornamental potential. Acta Hort. 683: 197–200.

Ratter, J. A., J. F. Ribeiro & S. Bridgewater. 1997. The Brazilian cerrado vegetation and threats to its biodiversity. Ann. Bot. 80: 223–230.

Renner, S. S. 1986–1987. Reproductive biology of *Bellucia* (Melastomataceae). Acta Amazon. 16/17: 197–208.

Renner, S. S. 1989. A survey of reproductive biology in Neotropical Melastomataceae and Memecylaceae. Ann. Missouri Bot. Gard. 76: 496–518.

Renner, S. S. 2004. Bayesian analysis of combined chloroplast loci, using multiple calibrations, supports the recent arrival of melastomataceae in Africa and Madagascar. Amer. J. Bot. 91: 1427–1435.

Renner, S. S., G. Clausing & K. Meyer. 2001. Historical biogeography of Melastomataceae: The roles of tertiary migration and long-distance dispersal. Amer. J. Bot. 88: 1290–1300.

Restrepo, C. & N. Gómez. 1998. Responses of understory birds to anthropogenic edges in a Neotropical montane forest. Ecol. Applic. 8: 170–183.

Restrepo, C., N. Gomez & S. Heredia. 1999. Anthropogenic edges, treefall gaps, and fruit-frugivore interactions in a neotropical montane forest. Ecology 80: 668–685.

Ribeiro, M. C., J. P. Metzger, A. C. Martensen, F. J. Ponzoni & M. M. Hirota. 2009. The Brazilian Atlantic forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biol. Conservation 142: 1141–1153.

Rico-Gray, V. & P. S. Oliveira. 2007. The Ecology and Evolution of Ant-Plant Interactions. The University of Chicago Press, Chicago.

Rodrigues, E. R. S. & F. A. O. Silveira. 2013. Seed germination requirements of *Trembleya laniflora* (Melastomataceae), an endemic species from Neotropical montane rocky savannas. Pl. Species Biol. 28: 165–168.

Rodrigues, R. R., R. A. F. Lima, S. Gandolfi & A. G. Nave. 2009. On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic forest. Biol. Conservation 142: 1242–1255.

Romero, R. & A. B. Martins. 2002. Melastomataceae do Parque Nacional da Serra da Canastra, Minas Gerais, Brasil. Revista Brasil. Bot. 25: 19–24.

Salazar, A., G. Goldstein, A. C. Franco & F. Miralles-Wilhelm. 2011. Timing of seed dispersal and dormancy, rather than persistence in soil seed-banks, control recruitment of woody plants in Neotropical savannas. Seed Sci. Res. 21: 103–116.

Samuels, I. A. & D. J. Levey. 2005. Effects of gut passage on seed germination: Do experiments answer the questions they ask? Funct. Ecol. 19: 365–368.

Santos, B., C. Peres, M. Oliveira, A. Grillo, C. Alves-Costa & M. Tabarelli. 2008. Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. Biol. Conservation 141: 249–260.

Santos, J. C., C. I. R. Santos, J. E. Cares & J. S. Almeida-Cortez. 2012. Impact of nematode-induced galls on

Miconia prasina (Sw.) DC (Melastomataceae) traits in the Atlantic forest of northeastern Brazil. J. Pl. Interac. 7: 1–7.

Sassaki R. M., J. N. Rondon, L. B. P. Zaidan & G. M. Felippe. 1999. Number of buried seeds and seedlings emergence in cerradao, cerrado and gallery forest soils at Pedregulho, Itirapina (SP), Brazil. Revista Brasil. Bot. 22: 147–152.

Schupp, E. W., P. Jordano & J. M. Goméz. 2010. Seed dispersal effectiveness revisited: A conceptual review. New Phytol. 188: 333–353.

Seixas, C. D. S., R. W. Barreto, L. G. Freitas, L. A. Maffia & F. T. Monteiro. 2004. *Ditylenchus drepanocercus*, a potential biological control agent for *Miconia calvescens* (Melastomataceae): Host-specificity and epidemiology. Biol. Control 31: 29–37.

Silva, J. M. C. & M. Tabarelli. 2000. Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. Nature 404: 72–74.

Silva, P. S. D., I. R. Leal, R. Wirth & M. Tabarelli. 2007. Harvesting of *Protium heptaphyllum* Aublet (March.) seeds (Burseraceae) by the leaf-cuting ant *Atta sexdens* L. promotes seed aggregation and seedling mortality. Revista Brasil. Bot. 30: 553–560.

Silva, P. S. D., A. G. D. Bieber, I. R. Leal, R. Wirth & M. Tabarelli. 2009. Decreasing abundance of leaf-cutting ants across a chronosequence of advancing Atlantic forest regeneration. J. Trop. Ecol. 25: 223–227.

Silva, W. R., P. de Marco, Jr., E. Hasui & V. S. M. Gomes. 2002. Patterns of fruit-frugivore interactions in two Atlantic forest bird communities of South-eastern Brazil: Implications for conservation. Pp. 423–435 *in* D. J. Levey, W. R. Silva & M. Galetti (editors), Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. CABI Publishing, Wallingford.

Silveira, F. A. O. 2011. Evolutionary ecophysiology of seed dormancy and germination of Melastomataceae from rupestrian grasslands. Ph.D. Thesis, Universidade Federal de Minas Gerais, Minas Gerais.

Silveira, F. A. O., D. Negreiros & G. W. Fernandes. 2004. Influência da luz e da temperatura na germinação de sementes de *Marcetia taxifolia* (A. St.-Hil.) DC. (Melastomataceae). Acta Bot. Brasil. 18: 847–851.

Silveira, F. A. O., P. O. Mafia, J. P. Lemos-Filho & G. W. Fernandes. 2012a. Species-specific outcomes of avian gut passage on germination of melastome seeds. Pl. Ecol. Evol. 145: 350–355.

Silveira, F. A. O., R. C. Ribeiro, D. M. T. Oliveira, G. W. Fernandes & J. P. Lemos-Filho. 2012b. Evolution of physiological dormancy multiple times in Melastomataceae from Neotropical montane vegetation. Seed Sci. Res. 22: 37–44.

Simão, E. & M. Takaki. 2008. Effect of light and temperature on seed germination in *Tibouchina mutabilis* (Vell.) Cogn. (Melastomataceae). Biota Neotrop. 8, <http://www.biotaneotropica.org.br/v8n2/en/abstract?article+bn00908022008>, accessed 26 June 2012.

Simão, E., A. T. Nakamura & M. Takaki. 2007. Época de colheita e capacidade germinativa de sementes de *Tibouchina mutabilis* (Vell.) Cogn. (Melastomataceae). Biota Neotrop. 7: 67–73.

Simon, M. F., R. Grether, L. P. Queiroz, C. Skema, R. T. Pennington & C. E. Hughes. 2009. Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. PNAS 106: 20359–20364.

Snow, D. W. 1965. A possible selective factor in the evolution of fruiting seasons in tropical forests. Oikos 15: 274–281.

Stiles, F. G. & L. Rosselli. 1993. Consumption of fruits of the Melastomataceae by birds: How diffuse is coevolution? Vegetatio 108: 57–73.

Tabarelli, M., A. V. Lopes & C. A. Peres. 2008. Edge-effects drive tropical forest fragments towards an early-successional system. Biotropica 40: 657–661.

Talora, D. C. & L. P. C. Morellato. 2000. Fenologia de espécies arbóreas em floresta de planície litorânea do sudeste do Brasil. Revista Brasil. Bot. 23: 13–26.

Thompson, K. & M. K. J. Ooi. 2013. Germination and dormancy breaking: Two different things. Seed Sci. Res. 23: 1.

Thompson, K., R. M. Ceriani, J. P. Bakker & R. M. Bekker. 2003. Are seed dormancy and persistence in soil related? Seed Sci. Res. 13: 97–100.

Traveset, A., A. W. Robertson & J. Rodríguez-Pérez. 2007. A review on the role of endozoochory in seed germination. Pp. 78–103 *in* A. J. Dennis, E. W. Schupp, R. J. Green & D. A. Westcott (editors), Seed Dispersal Theory and Its Application in a Changing World. CABI Publishing, Oxfordshire.

Urbas, P., M. V. Araújo, I. R. Leal & R. Wirth. 2007. Cutting more from cut forests: Edge effects on foraging and herbivory of leaf-cutting ants in Brazil. Biotropica 39: 489–495.

Urcelay, C., P. A. Tecco & F. Chiarini. 2005. Micorrizas arbusculares del tipo 'Arum' y 'Paris' y endófitos radicales septados oscuros en *Miconia ioneura* y *Tibouchina paratropica* (Melastomataceae). Bol. Soc. Argent. Bot. 40: 151–155.

Valdivia, C. E. & J. A. Simonetti. 2007. Decreased frugivory and seed germination rate do not reduce seedling recruitment rates of *Aristotelia chilensis* in a fragmented forest. Biodivers. & Conservation 16: 1593–1602.

Válio, I. F. M. & F. M. Scarpa. 2001. Germination of seeds of tropical pioneer species under controlled and natural conditions. Revista Brasil. Bot. 24: 79–84.

Vasconcelos, M. U., R. M. O. Lima, N. C. Robles, F. A. O. Silveira & G. W. Fernandes. 2007. Germinação de sementes de espécies de *Marcetia* DC. (Melastomataceae). *In* VIII Congresso de Ecologia do Brasil, Caxambú.

Vázques-Yanes, C. & A. Orozco-Segovia. 1993. Patterns of seed longevity and germination in the tropical rainforest. Annual Rev. Ecol. Syst. 24: 69–87.

Verdú, M. & A. Traveset. 2005. Early emergence enhances plant fitness: A phylogenetically controlled meta-analysis. Ecology 86: 1385–1394.

Viana, L. R., F. A. O. Silveira, J. C. Santos, L. H. Rosa, J. E. Cares, A. C. Café-Filho & G. W. Fernandes. 2013. Nematode-induced galls in *Miconia albicans*: Effect of host plant density and correlations with performance. Pl. Sp. Biol. 28: 63–69.

Zaia, J. E. & M. Takaki. 1998. Estudo da germinação de sementes de espécies arbóreas pioneiras: *Tibouchina pulchra* Cogn. e *Tibouchina granulosa* Cogn. Acta Bot. Brasil. 12: 221–229.

Zaia, J. E. & M. Takaki. 1999. A relação V/Ve da radiação solar difusa sob o dossel de uma área de Mata Atlântica. Acta Bot. Brasil. 13: 43–48.